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EMBRYOLOGY.[1]

Development of Mammals.—In so thoroughly worked over and so narrowly bounded a field as vertebrate embryology we should hope to find a singleness of plan running through the series, accompanied by an agreement amongst workers and theorists as to the interpretation of the known phenomena. In fact, however, the greatest possible divergence is found. This is especially marked in the recent attempts of embryologists to explain the process of gastrulation in the groups of vertebrates. Of course the problem of the mesoblast is here, as everywhere, a challenge for battle; but this is not all, for even the origin of endoderm and ectoderm have their various interpreters.

An illustration of this is furnished by the three (and more) hypotheses which are advanced to account for the early stages of development of the mammals. Two of these may be taken here as an example, and a third will be mentioned below in a review of Hubrecht's recent paper. The two which we shall now consider are those of Haddon[2] and Minot.[3] These two theories, advanced about the same time, are said by Haddon to be "somewhat similar hypotheses," and Minot says that his own is "the most satisfactory, and preferable to the similar explanation advanced . . . by Haddon." To an outsider the two theories seem to contradict each other in all that is essential and new to each.

Balfour prophesied that the ancestral mammal had a large ovum filled with yolk, and this, by Caldwell's discovery of the eggs of Monotremes, has been practically demonstrated. Both Haddon and Minot accept this as their starting point, but immediately diverge in opposite directions in their "somewhat similar explanations."

The two accompanying diagrams have been copied to illustrate their views:

Diagram *A* gives Haddon's idea of the meaning of the germ-layers of the mammalian embryo. The central cavity (*y.s.*) is the yolk-sac of the ancestral vertebrate, which has been covered over *precociously* by ectoderm (*e.c.*); ancestrally this was accomplished by epibole. At the upper pole the blastoderm, owing to the loss of yolk, has fallen into the yolk-cavity, leaving a small opening (*B b*) at the surface, which Van Beneden mistook for the blastopore. The blastoderm proper consists of ectoderm, several cells in thickness, and below scattered endoderm cells. The mesoderm is formed later between the two. The strong point of this explanation is that it seems to refer the germ-layers back to a condition found in the reptilian embryo, and the weak point, it seems to me, is that it does not clearly illustrate the method by which the yolk has been lost, and what cells originally contained it.

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[1] Edited by T. H. Morgan, Johns Hopkins University, Baltimore.

[2] Elements of Embryology.

[3] AMERICAN NATURALIST, April, 1889.

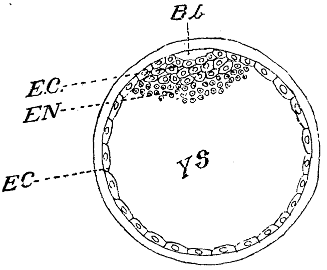

FIG. 1.—(Diagram A.)

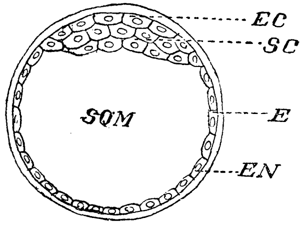

FIG. 2.—(Diagram B.)

Minot gives the following hypothetical stage to explain the homologies of the mammalian germ-layers (see Diagram *B*). The large central cavity, which he calls the segmentation cavity (the yolk-cavity of Haddon), is surrounded by *endodermal* cells, which formerly contained yolk. (Hence they do not represent epibolic ectoderm, as believed by Haddon.) The walled blastoderm (embryonic knob) at the upper pole of the figure is composed probably *entirely* of *ectoderm cells*. (Again a contradiction to Haddon's view.) The endoderm which later appears under the blastoderm comes from the sides where the endoderm cells around the segmentation cavity pass into the ectodermal blastoderm. Here, it seems to me, is the weakest part of the hypothesis, and Dr. Minot seems to have expected to find the same formation of endoderm as in the teleost. This is flatly contradicted by well-supported statements. (See Hubrecht below.) The author has jumped from the frog's gastrula to that of the mammal, not giving, I believe, due weight to the intermediate reptilian stage, assuming that with the loss of yolk in the ancestral mammal there was a return to the more primitive condition of the amphibian stage; but it seems this is hardly a fair assumption as a basis for further hypotheses.

Prof. Hubrecht gives a second paper[4] in his studies in mammalian embryology, entitled "The Development of the Germinal Layers of

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[4] *Quar. Jour. Micro. Science.*

Sorex vulgaris." The paper is a detailed description of the origin of the germ-layers. The earliest stage obtained had a single layer of flattened cells (ectoderm) lying beneath the zona and bounding a central cavity filled with fluid. These ectodermal cells he calls the trophoblast. At one point in the periphery there is an accumulation of cells —the embryonic knob—which contains the material for the embryonic ectoderm and endoderm. The cavity in the center surrounded by the trophoblast and filled with fluid is the *segmentation cavity*. The embryonic knob gives rise to the early endoderm cells from its more central part, and some of these then migrate around the periphery of the central cavity and apply themselves to the inner side of the trophoblast (ectoderm). See Diagram *C*. (This contradicts part of Minot's hypothesis given above.) The trophoblast cells seem to grow over the embryonic knob, causing an "inversion" of the embryo. After the differentiation of the endoderm from the embryonic knob the remaining ectoderm is spoken of as the embryonic shield (*emb.sh.*) The endoderm first forms part of the notochord and mesoblastic plates. Thus under the anterior end of the embryonic shield the endoderm is spoken of as the protochordal plate (*no.ch'.*) The rest of the notochord differentiates later and in a different way. The mesoderm has not yet appeared, but is now inaugurated by the appearance of the primitive streak. The mesoderm originates from three different points: 1st, from the sides of the protochordal plate (see above); 2nd, from the primitive streak, from which it advances forward between ecto- and endoderm; and 3d, from an annular zone of endoderm lying around and under the periphery of the embryonic shield. The details of this process are shown in a large number of figures.

We may now pass to the theoretical considerations of the gastrulation of mammals. (The process of inversion, or the sinking of the embryo into the cavity of the vesicle, may be left out of account, as it produces no important changes in the germ-layers of the embryo, and may in a general way be compared with the later formation of the amnion.) We have seen in the early differentiation of the endoderm from the embryonic knob that part of the endoderm is formed before the actual process of gastrulation has set in,—that is, before the appearance of the primitive streak. This the author calls precocious segregation, and is an *ontogenetic* phenomenon. Later, when the primitive streak is formed (the coalescing of the lips of the blastopore), new endoderm arises in this region and is added to that already present, and this latter is the phylogenetic endoderm, and alone is to be compared to the Sauropsidan type. The remaining part of the notochord (also the lateral wings of the mesoderm) is formed from the phylogenetic endoderm, and may be compared to the formation of notochord and mesoblast of Batrachia.

We have sufficient evidence to believe that between the Batrachia and the Mammalia a "phylogenetic link has once existed, in which the actual food-yolk formed a very considerable addition to the early blastocyst. The case of the Ornithodelphia is most important in this respect. . . . When the nutritive contents of the yolk-sac were no longer of primary importance, . . . a reduction in size of the blastocyst was not effectuated because *another factor came into play.* The vascular area which heredity called forth on the surface of the yolk-sac . . . must have rendered eminent service for the establishment of a different mode of nutrition, as soon as the embryo underwent a considerable part of its development inside the maternal generative ducts." Hence the large size of the blastocyst of the mammal has been *retained not because it once contained yolk*, but because it was an essential function to perform in the nutrition of the embryo.

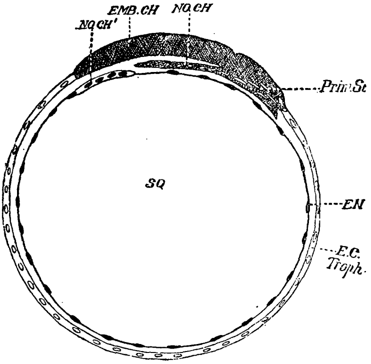

FIG. 3.—(Diagram C.)

The accompanying diagram (Fig. 3) represents (somewhat modified) the author's figure to show the relationship to each other of the mammalian germ-layers. The greater part of the central (fluid) cavity is surrounded by two layers,—the outer of ectoderm, the trophoblast, and within the ontogentic endoderm. The upper part of the figure shows the embryonic layers. The endoderm passes under the ectodermal embryonic shield (black). The posterior part of the latter (with white streaks) shows the area of the primitive streak, and from this runs forward under the embryonic shield a prolongation (*no.ch.*, black with white dots), forming the posterior part of the notochord, and laterally, though not shown in the figure, the wings of mesoblast. In front of this is seen a thickened part of the ontogenetic endoderm, which forms precociously the anterior end of the notochord (*no.ch.*) and to the sides some of the mesoderm. For further details see the author's excellent figures.

The essential difference between this hypothesis and that of Minot is at once seen. What the latter speaks of as endoderm cells are the trophoblast cells of Hubrecht, which are ectodermal. Hubrecht shows conclusively that the endoderm originates from the embryonic knob, and not at its sides as is demanded by Minot's recent hypothesis. Hubrecht is more in accordance with Haddon, both as to the origin of the endodern from the under side of the embryonic shield, and in the ectodermal covering of the the early blastocyst.—T. H. M.

The Embryology of Gecko.—Dr. Ludwig Will gives, in the *Biologisches Centralblatt*, November 15, 1890, a short paper on the method of gastrulation of this lizard. At the posterior end of the embryonic shield is a mass of cells, called the primitive plate. The cells at this point are several rows deep, while over the embryonic shield the ectoderm is composed of a single layer of columnar cells, but with a few yolk-cells scattered beneath it. At a later stage the anterior end of the primitive plate forms a distinct invagination, the walls formed of a single row of cells. This sac pushes forward under the embryonic shield, between the ectoderm and the yolk-cells. The invagination cells spread out into a broad sac. There follows next an irregular fusion and absorbtion between the invaginated endoderm and the yolk-cells (endoderm also), so that the general cavity above the yolk, in which the yolk-cells were scattered, communicates with the invagination cavity, and hence with the outer world by means of the proximal end of the latter cavity, or blastopore. The upper walls of the invaginated cells go to form the notochord, and the rest of them go to form the mesoderm at the sides of the latter. The author believes that the Gecko furnishes grounds for comparing the reptilian with the amphibian gastrulation. The blastopore—or the open mouth of the invagination—extends backwards, and the two lips coming in contact fuse to form a primitive streak, so that what was previously only a theory—namely, that the primitive streak was formed by the fusion of the lips of the blastopore in Sauropsida, and whose opening in these was only represented by the neurenteric canal—is now shown to be a fact from the development of the Gecko.

Theory of the Mesoderm.[5]—Prof. C. Rabl has a long paper on the origin of the mesoderm of vertebrates. The paper is largely devoted to theoretical discussions, although based upon observations on the germ-layers of Selachians, birds, and mammals. The first part of the paper deals with the formation of the mesoderm in the above types, the second with the later differentiations of the mesoderm. It is unnecessary to give a full review of the paper here,[9] and we may confine

[5] *Morphologisches Jahrbuch*, No. 15, 1889.

See *Journ. Royal. Micro. Soc.*, Feb., 1890.

our attention to that part of it dealing with the gastrulation of the vertebrates. The Selachian gastrulation arose by the accumulation of yolk in the cyclostome egg, while the Amniote (reptiles, birds, mammals) gastrula arose from accumulated yolk to the amphibian egg. The resulting gastrulæ of Selachians and Amniota, the author attempts to show, are therefore fundamentally different. The Selachian (and Teleost) gastrulæ resulted from the addition of yolk to the endoderm cells of the cyclostome before the ectoderm had grown over the endoderm, and since the epibolic endoderm does not cover in the yolk, the blastopore in this group is represented by the whole margin of the embryonic shield. The blastopore mouth then is very large, and the (morphological) posterior end of the blastopore lies just in front of the embryonic shield, and the anterior or upper end of the blastopore lies at its usual position at the posterior end of the shield. This is, of course, the general conception. But for the Amniota the author believes the gastrula to be different in that it is not here represented by the whole border of the embryonic shield, but has a more limited extent. Rabl believes that the accumulation of yolk in the amphibian egg has been also in the endoderm cells, but, so far as he explains it, this must have taken place after (ancestrally) the epiblast had covered the (endoderm) yolk-mass so that the gastrula becomes reduced to the region of the primitive streak alone. Therefore it follows that one end of the primitive groove (just behind the embryonic shield) represents the anterior (upper) end of the amphibian blastopore, and the other end of the groove the posterior (lower of the amphibian). The anterior end of the primitive shield would not seem here to represent anything in particular ! Rabl supports his conclusion by arguments drawn from the formation of the mesoderm.

The author does not account for the large exposure of yolk outside of the blastopore in the Amniota gastrula as we find it in the bird and lizard ; unless indeed he supposed it to have actually broken through the ectoderm covering. Further, that the author's view is probably erroneous is shown in the occasional presence of a lengthened primitive streak running posteriorly through the area opaca, as seen and figured by Whitman. It has also, I believe, been seen since by others.